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Variation in Shoot Organization in *Prunus* (Rosaceae) with Special Reference to *Prunus ogawana*

Akitoshi IWAMOTO[a], Keiko MIYAZAKI[b] and Jin MURATA[c]

[a]University Museum, the University of Tokyo,
Hongo 7–3–1, Bunkyo-ku, Tokyo, 113-0033 JAPAN;
[b]Makino Herbarium, Tokyo Metropolitan University,
Minamiosawa 1–1, Hachioji, Tokyo, 192-0397 JAPAN;
[Present address: Matsubara 3–39–29, Setagaya-ku, Tokyo, 156-0043 JAPAN]
[c]Botanical Gardens, Graduate School of Science, the University of Tokyo,
Hakusan 3–7–1, Bunkyo-ku, Tokyo, 112-0001 JAPAN

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To determine variation in shoot development in *Prunus* (Rosaceae), we observed and compared the shoot organization of 13 species (9 species of subgen. Cerasus sect. Pseudocerasus; 1 species of sect. Microcerasus; 1 species of sect. Phyllomahaleb; 1 species of subgen. Prunus; and 1 species of subgen. Padus). As a result, we can categorize the observed species into four distinct groups based on shoot organization of 1) types of winter bud growth, 2) growth of buds in the axils of scale-like prophylls, and 3) shoot abscission. The first group includes all species of subgen. Cerasus sect. Pseudocerasus and sect. Phyllomahaleb except *P. ogawana.* The second group includes only *P. ogawana*, the third group contains *P. mume* and *P. glandulosa*, and the fourth group contains only *P. grayana*. *Prunus ogawana* (subgen. Cerasus sect. Pseudocerasus) is distinct from other members of sect. Pseudocerasus in that some winter buds develop into mixed shoots producing both flowers and leaves, and some buds in the axils of scall-like prophylls grow into vegetative shoots. In addition, this grouping is basically supported by the phylogenetic DNA analysis of *Prunus.*

Key words: *Prunus*, *Prunus ogawana*, *Prunus* subgenus Cerasus, shoot organization

Introduction

Prunus (Rosaceae), comprising about 200 species, has been usually classified into several subgenera (Rehder 1940, Gohra and Panigrahi 1995). Ohba (1989) recognized five subgenera (Prunus, Amygdalus, Padus, Laurocerasus, Cerasus) in Japan. There are some references to shoot organization in *Prunus* in the descriptions of the species, but critical comparative studies have not been conducted. We observed the shoot organization of species of 13 *Prunus* (mainly Japanese wild species) to compare them and to determine the degree of variation between them. We especially focused on *P. ogawana* Makino (subgen. Cerasus sect. Pseudocerasus). The species usually blossoms within three years of germination (Makino 1906), while other species of *Prunus* usually need 10–15 years for flowering. Additionally, the species produces fertile seeds that can relatively easily propagate. Hence, *Prunus ogawana* was expected to be suitable for experimental studies of flower formation in *Prunus* using genetic recombinant methods.

Flowering at a juvenile stage has been

considered to be the only distinct characteristic differentiating it from other species of sect. Pseudocerasus. Our preliminary observations revealed that all winter buds develop into shoots with flowers. This feature does not occur in other species of *Prunus* and shows that the shoot organization of *P. ogawana* may be unique. Detailed observations of shoot organization in *P. ogawana* and of other phylogenetically closely related species of *Prunus* are necessary to ascertain that the feature is species-specific.

Materials and Methods

We observed shoots of 13 species of *Prunus* throughout two years (from April 1998 to March 2000) using living trees and sample branches obtained from the trees. Among 13 species, nine belong to subgenus Cerasus sect. Pseudocerasus, the other four belong to: subgen. Prunus (*P. mume*), subgen. Padus (*P. grayana*), subgen. Cerasus sect. Microcerasus (*P. glandulosa*) and subgen. Cerasus sect. Phyllomahaleb (*P. maximowiczii*). The materials used in this study are shown in Table 1. We observed details of the shoots macrographically. A stereoscopic microscope was used to observe axillary bud organization.

Results

Features observed

We determined that three features were important for analyzing shoot organization; (1) type of winter bud growth, (2) growth of buds in the axils of scale-like prophylls and (3) shoot abscission. Observations of each item are as follows:

(1) Types of winter bud growth

All the species examined in this study are deciduous and all new shoots extend from winter buds. The winter buds of species of *Prunus* usually develop into one of three types: (1) a vegetative shoot that produces some leaves and no flowers, (2) a reproduc-

Table 1. Observed materials of *Prunus* s. l. in this study. Scientific names are arranged according to Ohba (1989)

Subgenus	Section	Species	Source*			
Cerasus	Phyllomahaleb	*maximowiczii* Rupr.				IV
	Pseudocerasus	*apetala* (Siebold & Zucc.) Franch. & Sav.				IV
		cerasoides D. Don var. *campanulata* (Maxim.) Koidz.				IV
		incisa Thunb.	I			IV
		jamasakura Siebold ex Koidz.	I	II	III	IV
		pendula Maxim. f. *ascendens* (Makino) Ohwi	I			IV
		sargentii Rehder	I			IV
		speciosa (Koidz.) Nakai				IV
		verecunda (Koidz.) Koehne	I		III	IV
		ogawana Makino	I	II		
	Microcerasus	*glandulosa* Thunb.				IV
Prunus		*mume* (Siebold) Siebold & Zucc.				IV
Padus		*grayana* Maxim.	I			IV

*Source. I: Tokyo Metropolitan University. II: Botanical Gardens Koishikawa, Graduate School of Science, the University of Tokyo. III: Botanical Gardens Nikko, Graduate School of Science, the University of Tokyo. IV: Tama Forest Science Garden.

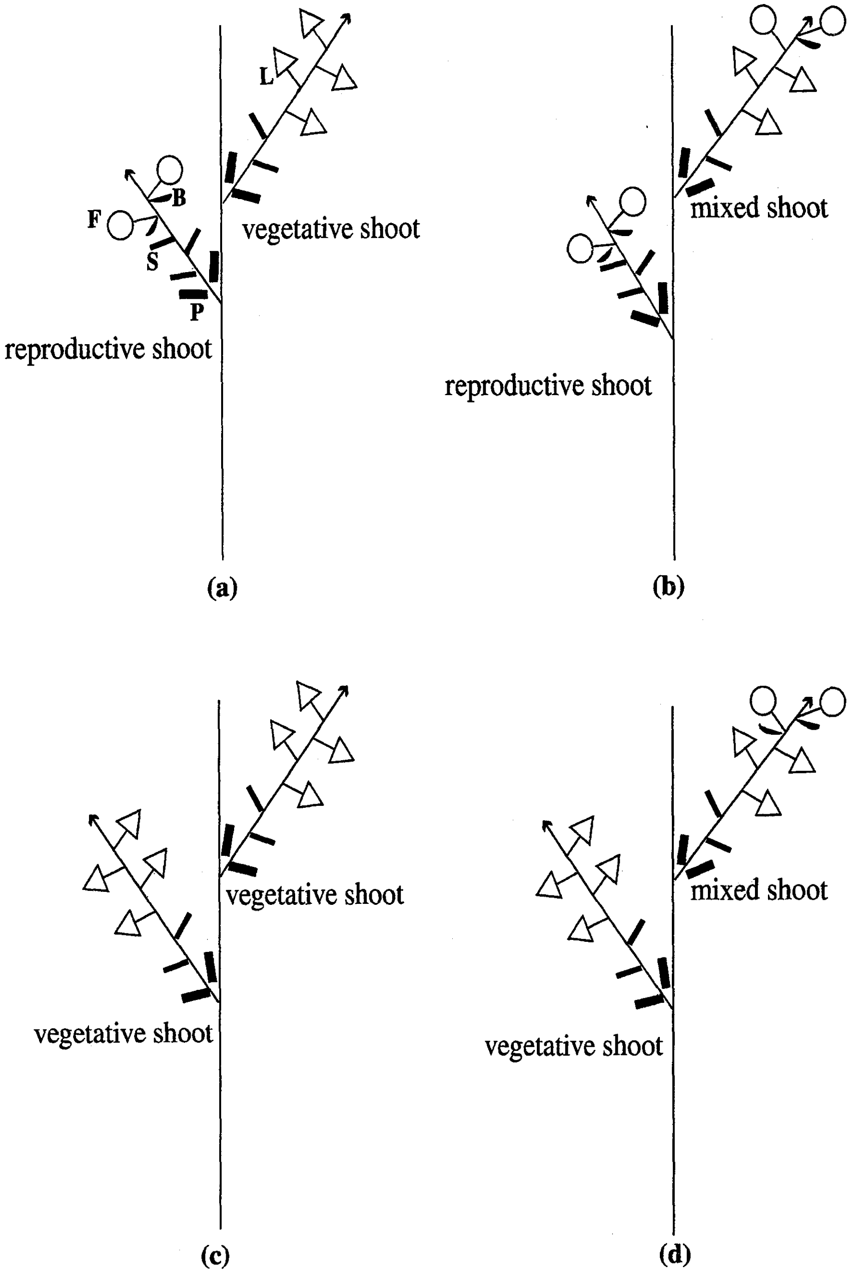

Fig. 1. Types of winter bud growth in *Prunus* s. l. (a) Winter buds grow into both reproductive shoots and vegetative shoots. (b) All winter buds grow into shoots with flowers. Some shoots also develop leaves (mixed shoots). (c) Winter buds grow into only vegetative shoots. (d) All winter buds grow into shoots with leaves. F: flower. B: bract. L: leaf. S: scale-like leaf. P: scale-like prophylls of winter buds. Arrows indicate indefinite shoots.

tive shoot that produce some flowers and no leaves or (3) a mixed shoot that produce both flowers and leaves. We also found that the species of *Prunus* produce three kinds of winter buds in various combinations, which are illustrated in Fig. 1.

(a) Growth into reproductive shoots and vegetative shoots

Winter buds produce a reproductive shoot and a vegetative shoot in this type. No buds develop into a mixed shoot. An apical bud is more likely than a lateral one to grow into a vegetative shoot. The species that show this type are *P. jamasakura*, *P. verecunda*, *P. sargentii*, *P. speciosa*, *P. pendula*, *P. cerasoides*, *P. incisa*, *P. apelata* and *P. maximowiczii.*

(b) Growth into reproductive shoots and mixed shoots

All winter buds produce flowers. In addition, some of them also develop some leaves, but buds in the axils of scale-like prophyll show shoot elongation of another type (see (2) *Growth of buds in the axil of scale-like prophylls*). The species showing this type is *P. ogawana.*

(c) Growth into only vegetative shoots

All winter buds grow into vegetative shoots in this type and no shoots with flowers were found. Buds in the axils of scale-like prophylls also show shoot elongation of another type (see (2) *Growth of buds in the axil of scale-like prophylls*). The species which show this type are *P. mume* and *P. glandulosa.*

(d) Growth into vegetative shoots and mixed shoots

All winter buds develop leaves and sometimes also produce some flowers. The species showing this type is *P. grayana.*

(2) Growth of buds in the axils of scale-like prophylls

Some species of *Prunus* have buds in the axils of scale-like prophylls of the winter buds (we call the bud in the axil of a leaf the main bud to distinguish it from the buds in the axils of scale-like prophylls) (Fig. 2). The prophyll buds do not appear to expand soon, but a study by Guo et al. (1992) implied that such buds in *P. persica* regularly develop into shoots. Our observations revealed that the axillary buds show a variety

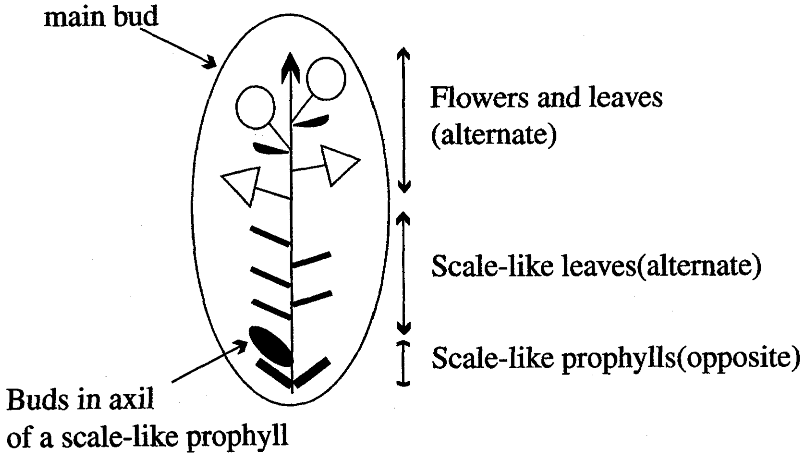

Fig. 2. Structure of winter bud (a mixed bud) in *Prunus* s. l. Flower buds produce no leaves and vegetative buds produce no flowers. Meaning of symbols are same as those in Fig. 1.

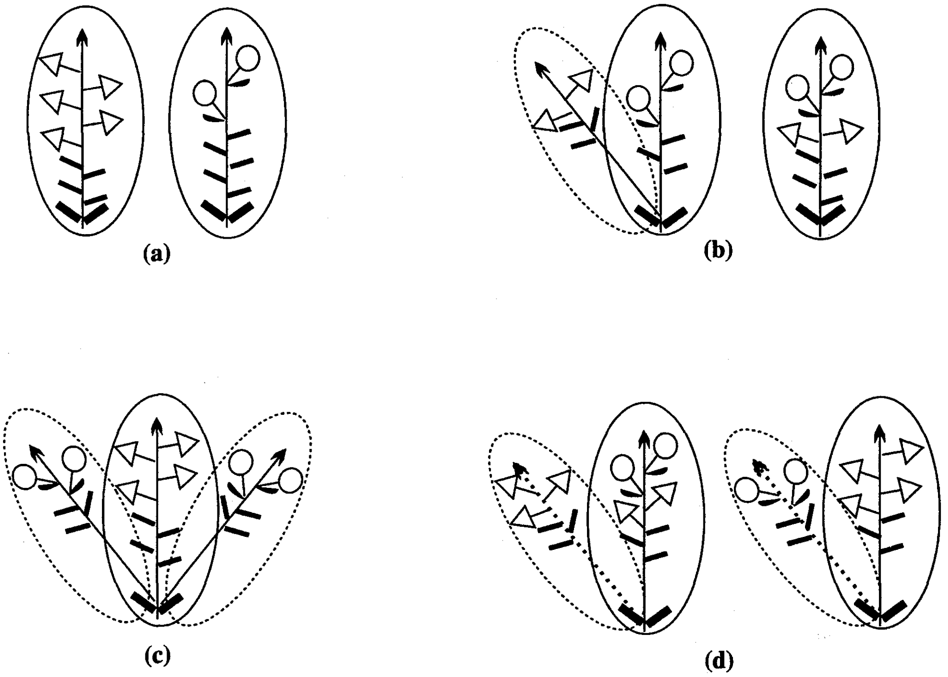

Fig. 3. Growth of buds in the axil of scale-like prophylls in *Prunus* s. l. (a) Buds in the axile of scale-like prophylls do not develop. (b) Buds in the axile of scale-like prophylls of mixed shoots develop into vegetative shoots. (c) All buds in the axile of scale-like prophylls develop into reproductive shoots. (d) Buds in the axil of scale-like prophylls develop vegetative and mixed shoots in following year. Shoots indicated by broken lines extend one year after shoots in solid lines develop. Shoots within solid ellipse are derived from main buds; shoots in broken ellipse extend from buds in axil of scale-like prophylls of main buds. Meaning of symbols are same as those in Fig. 1.

of growth patterns, for which we can distinguish four types (Fig. 3).

(a) Buds in the axils of scale-like prophylls not developing

Axillary buds were recognizable rarely in the axils of winter scale-like prophylls, or if they were present the bud hardly expands. The species exhibiting this type are *P. jamasakura*, *P. verecunda*, *P. sargentii*, *P. speciosa*, *P. pendula*, *P. cerasoides*, *P. incisa*, *P. apelata* and *P. maximowiczii.*

(b) Some buds in the axils of scale-like prophylls develop into vegetative shoots

The bud in the axil of scale-like prophylls of a new shoot sometimes grows into a vegetative shoot in the same year as the new shoot. Shoots which have no leaves were more likely to develop these axillary vegetative shoots than shoots with leaves. A single bud in either axil of two scale-like prophylls grows into a vegetative shoot. The species showing this type is *P. ogawana.*

(c) All buds in the axils of scale-like prophylls develop into reproductive shoots

Almost all buds in the axils of the scale-like prophylls grow into reproductive shoots. Buds in both axils of two scale-like prophylls expand. They also grow into shoots in the same year when the main buds developed. The species showing this type are *P. mume* and *P. glandulosa.*

(d) All buds in the axils of scale-like

prophylls develop into new winter buds

Nearly all buds in the axils of the scale-like prophylls develop into winter buds that grow into vegetative or mixed shoots in the following year of main bud expansion. A single bud in either axil of two scale-like prophylls grows into a vegetative shoot or mixed shoot. That is, buds in the axils of scale-like prophylls become new winter buds. The species with this type is *P. grayana.*

(3) Shoot abscission

Species of *Prunus* usually abscise reproductive shoots by the end of the flower season, while vegetative shoots persist. But extraordinary abscission has been reported in *P. grayana.* Our observations also revealed variation in shoot abscission patterns in this species. We recognized three types in this character (Fig. 4).

(a) Reproductive shoots abscising; vegetative shoots persisting

All reproductive shoots abscise by winter, while all vegetative shoots persist to develop new shoots from their axillary buds in the following year. The species showing this type are *P. jamasakura*, *P. verecunda*, *P. sargentii*, *P. speciosa*, *P. pendula*, *P. cerasoides*, *P. incisa*, *P. apelata*, *P. maximowiczii*, *P. mume* and *P. glandulosa.*

(b) Reproductive shoots abscising; vegetative and mixed shoots persisting

All reproductive shoots abscise and all vegetative shoots persist. In addition, mixed shoots also persist. That is, any shoots with leaves do not abscise. The species showing this type is *P. ogawana.*

(c) All shoots abscising

All shoots, irrespective of the type, usually abscise by the winter of the shoot extension except the terminal vegetative shoots. As a result, tree shape with a simple branching pattern is formed. The species exhibiting this type is *P. grayana.*

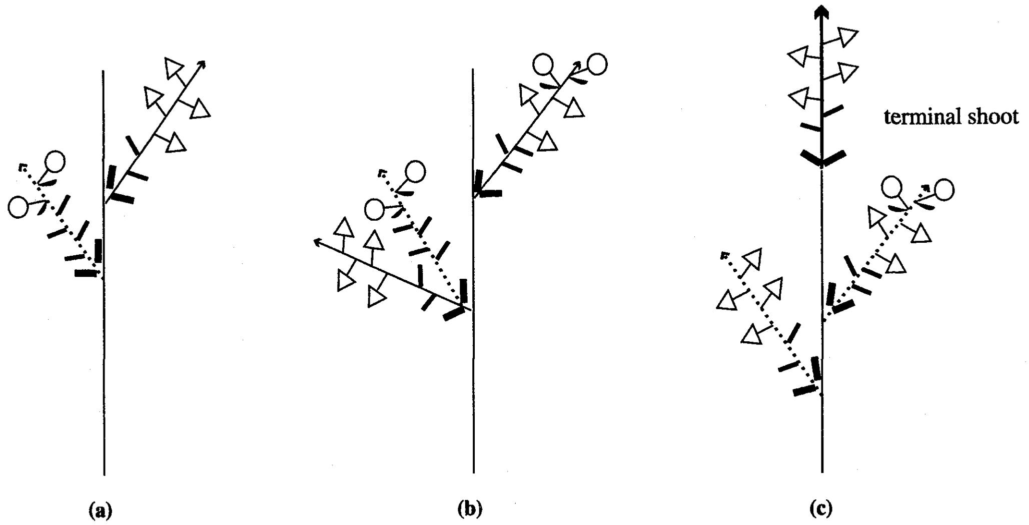

Fig. 4. Shoot abscission in *Prunus* s. l. (a) Reproductive shoots abscise, while vegetative shoots persist. (b) Mixed shoots and vegetative shoots persist. Reproductive shoots abscise. (c) All shoots except terminal ones abscise. Solid lined shoots persists and broken lined shoots abscise. Meaning of symbols are same as those in Fig. 1.

Table 2. Result of observation on *Prunus* s. l. in this study. Item 1: Types of winter bud growth. Item 2: Growth of buds in the axils of scale-like prophylls. Item 3: Shoot abscission. See the text for explanation of the Groups I–IV

Subgenus	Section	Species	Item 1	Item 2	Item 3	Group
Cerasus	Phyllomahaleb	*Prunus maximowiczii*	a	a	a	I
	Pseudocerasus	*P. apetala*	a	a	a	I
		P. cerasoides	a	a	a	I
		P. incisa	a	a	a	I
		P. jamasakura	a	a	a	I
		P. pendura	a	a	a	I
		P. sargentii	a	a	a	I
		P. speciosa	a	a	a	I
		P. verecunda	a	a	a	I
		P. ogawana	b	b	b	II
	Microcerasus	*P. glandulosa*	c	c	a	III
Prunus		*P. mume*	c	c	a	III
Padus		*P. grayana*	d	d	c	IV

Discussion

Grouping of observed species on the shoot organization

We can categorize the observed species into four groups based on our observation of the three types of shoot organization (Table 2). Detailed descriptions of each group are as follows:

Group I [*Prunus jamasakura, P. verecunda, P. sargentii, P. speciosa, P. pendula, P. cerasoides, P. incisa, P. apetala, P. maximowiczii*]

In these species the buds in the axils of leaves produce vegetative and reproductive shoots. Reproductive shoots abscise and vegetative shoots persist after flowering season. Buds in the axils of scale-like prophylls are not present or, if present, they do not develop.

Group II [*Prunus ogawana*]

All buds in the axils of leaves produce reproductive and mixed shoots (all shoots have flowers). The buds in the axil of scale-like prophylls in *P. ogawana* often develop into vegetative shoots. All reproductive shoots abscise, while the shoots with leaves (mixed and vegetative shoots) persist.

Group III [*Prunus mume, P. glandulosa*]

All winter buds develop into vegetative shoots and buds in the axils of scale-like prophylls develop into reproductive shoots simultaneously. All reproductive shoots abscise and all vegetative shoots persist.

Group IV [*Prunus grayana*]

Mixed shoots and vegetative shoots develop from winter buds. The winter buds are derived from smaller winter buds in the axils of scale-like prophylls. All shoots except the terminal ones usually abscise before winter.

Specific shoot organization of Prnus ogawana

Prunus ogawana is basically similar to other species of sect. Pseudocerasus and it was difficult to find any distinction between them except for the flowering of *P. ogawana* at a juvenile stage. For this reason, on the basis of similar morphology in the juvenile stage, Makino (1912), Ohwi (1952) and Sugimoto (1961) treated it as a form of *P.*

jamasakura. Our study, however, revealed that *P. ogawana* is far different from the other species in sect. Pseudocerasus in shoot organization (Table 2).

We consider *P. ogawana* to show specific shoot organization because all winter buds grow into shoots with flowers. Winter buds of other species of sect. Pseudocerasus usually develop into shoots with no flowers and shoots with some flowers and no leaves (reproductive) and some with just leaves (vegetative); the vegetative shoot is photosynthetic and contributes to vegetative growth. In *P. ogawana*, all winter buds develop into shoots with flowers. If all shoots had no leaves, as in the reproductive shoots of other species of sect. Pseudocerasus, *P. ogawana* would not develop leaves and could not photosynthesize. It is understandable, therefore, that *P. ogawana* develops leaves on reproductive shoots (= mixed shoots) and that buds in the axils of scale-like prophylls develop into leafy shoots for vegetative growth.

Shoot organization of Group I –genus Cerasus *Group*

Prunus is sometimes divided into several genera (Komarov 1971, Yü et al. 1986, Ohba 1992). Ohba (1992) united and raised subgenus Cerasus sections Pseudocerasus and Phyllomahaleb to the genus *Cerasus* for the Japanese species. A recent phylogenetic analysis using DNA sequences also showed the monophyly of *Cerasus* in the sense of Ohba (1992) (Lee and Wen 2001). In our study, all species of subgenus Cerasus sections Pseudocerasus, except *P. ogawana*, and Phyllomahaleb, are in Group I.

*Shoot organization of Group III –*Prunus mume *and* P. glandulosa

Our study showed that *P. mume* and *P. glandulosa* can be categorized into one category with the same shoot organization pattern. Previous studies on shoot organization of *P. persica* indicated that it has the same pattern (Guo et al. 1992, Kervella et al. 1995). Taxonomic studies based on morphology have classified these three species into three different subgenera of *Prunus* s. l., but the phylogenic analysis using DNA sequences shows their close relationship. Our study corroborates the results of that phylogenic analysis, but the number of species we analyzed is too few. Further analyses of shoot organization in additional species in the subgenera Prunus, Amygdalus and Cerasus sect. Microcerasus are needed.

Shoot organization of Prunus grayana

Prunus grayana shows distinct shoot organization. The most remarkable feature is the abscission of all shoots except the terminal ones. In other species, all shoots with leaves persist and the buds in the axils of their leaves develop into winter buds. In *P. grayana*, we observed that the buds in the axils of the leaves also expand and develop some leaf primordia, but all shoots with those axillary buds abscise by the end of the growing season. In other words, the development of buds in the leaf axils of non-terminal shoots appears to be of no use to the plant.

It is also a distinct character of *P. grayana* to develop mixed shoots as in *P. ogawana*, but, the features of development are not the same. While *P. ogawana* develops mixed shoots because of flowering in all shoots, *P. grayana* develops vegetative shoots as well. We therefore consider that there may be some developmental differences in the formation process of mixed shoots between *P. grayana* and *P. ogawana.*

Further study

The present study indicates the specificity of shoot organization of *P. ogawana.* It is especially important that *P. ogawana* develops leaves on its mixed shoots since the development of both flowers and leaves on the same shoot has never been observed in other species of genus *Cerasus* in the sense of Ohba (1992). The leaf development process in this species is expected to be different from other species in subgenus Cerasus, which will be examined and discussed in a forthcoming study.

Our results also indicate that shoot organization might be an important taxonomic feature for reevaluating *Prunus* s. l., since phylogenetic studies using DNA sequences have basically agreed with our groupings of species based on shoot organization. Extensive observation of shoot organization on additional species is needed.

Shoot organization in *P. grayana* also needs further analysis. From an evolutionary point of view, shoot abscission following bud growth in this species is very inefficient. It is difficult to understand how or why this pattern developed. Further ecological and evolutionary studies may provide an answer.

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岩元明敏[a]，宮崎慶子[b]，邑田　仁[c]：**バラ科サクラ属のシュート構成の多様性およびワカキノサクラの特異性について**

本研究ではバラ科サクラ属（*Prunus*）植物のシュート構成の多様性を明らかにするため，日本に自生する種を中心にサクラ属13種（サクラ亜属サクラ節10種，ミヤマザクラ節1種，ユスラウメ節1種，スモモ亜属1種，ウワミズザクラ亜属1種）について年間を通じた観察を行った．この結果，対象とした13種は（1）冬芽成長（2）冬芽の鱗片化した前出葉腋芽の発達・伸長（3）枝の脱落性という3つのシュート構成の特徴に注目することで，明確に4つのグループに分けられ，多様性が確認された．最初のグループには，ワカキノサクラを除くサクラ亜属サクラ節とミヤマザクラ節の9種が，2番目のグループにはワカキノサクラが，3番目のグループにはウメ及びニワザクラが，4番目のグループにはウワミズザクラがそれぞれ含まれた．ワカキノサクラは他のサクラ節植物とは異なるグループに属し，全てのシュートに花をつける，混成芽を持つ，前出葉腋芽が展開するなどシュート構成に大きな特異性を持つことが分かった．また，グループ分けが基本的にサクラ属についての分子系統解析と一致することから，シュート構成がサクラ属内の系統関係を反映している可能性も示唆された．

（[a]東京大学総合研究博物館，
[b]東京都立大学牧野標本館
現所属：慶応義塾高校講師，
[c]東京大学大学院理学系研究科附属植物園）